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BOTANICAL GAZETTE

MAY, 1904

THE EVOLUTION OF MONOCOTYLEDONS.

ETHEL SARGANT.

(WITH SIX FIGURES)

NO SUBJECT is of more general interest to botanists than the early race-history of angiosperms. In a recent paper¹ I have attempted to justify the publication of a new hypothesis on this subject by a detailed account of the embryological evidence on which it is founded. The details of such work, however, have little interest for any but specialists, and I wish to deal here with the wider aspects of the subject. The argument of the following pages is in substance that contributed to a discussion on the evolution of monocotyledons which was held in September, 1903, at the Southport meeting of the British Association for the Advancement of Science. The whole paper has been recast since then, much has been added, and something omitted; in particular several passages have been introduced in answer to objections raised during the discussion.

There is a remarkable absence of direct geological evidence concerning the origin of angiosperms and the comparative antiquity of the two races included in that group. In the present state of our knowledge all conclusions with regard to the race-history of angiosperms must be founded on the comparative morphology of living forms. On such grounds, however, I have ventured to assume that monocotyledons and dicotyledons will ultimately be traced back to a common ancestor which in all

¹SARGANT E., A theory of the origin of monocotyledons. *Annals of Botany* 17:1. 1903.

essential features was an angiosperm, in spite of the fact that several modern authorities hold the contrary opinion.²

The isolation of the angiosperms, long recognized, has been emphasized by recent work. On the one hand, the connection of gymnosperms with pteridophytes has been so far traced through forms now extinct that the degree of relationship between those groups can be estimated, while no link has been found to connect the angiosperms with any other group. Thus our ignorance of their genealogy is the more obvious by contrast with increasing knowledge concerning that of other vascular plants. On the other hand, the internal structure of the embryo sac both before and after fertilization has been shown of late to separate angiosperms from other forms even more completely than was formerly supposed.

The gulf which separates angiosperms from all other plants is indeed of unknown depth. By comparison the internal boundary which divides monocotyledons from dicotyledons is very insignificant. The points of resemblance between members of these two classes are far more numerous and more important than those in which they differ.

Translated into the language of evolution, this means that the angiosperms are a race of considerable antiquity, which at some epoch in its history gave rise to two branches, monocotyledons and dicotyledons. If this is the case, it is clearly a point of great importance to obtain some notion of the structure of the primitive angiospermous stock.

Whatever the primitive angiosperm may have been, we may fairly assume that it was not a perfect mean between the monocotyledon and dicotyledon, nor on the other hand totally unlike either. Which did it most resemble? In other words, which type is the more primitive?

This is no new problem. It has been debated for upwards of fifty years, and during that period most botanists have maintained the superior antiquity of monocotyledons. Of late this

²BALFOUR, I. B., Presidential address to section K of the British Association. 1901. COULTER, J. M., The phylogeny of angiosperms. Decennial Publ. of University of Chicago. 1903.

opinion has lost ground. The evidence which supports it has been criticised, and more than one observer has brought forward facts in favor of the claim of dicotyledons to be considered the elder branch.

EVIDENCE FOR THE PRIMITIVE MONOCOTYLEDON.

The case for monocotyledons rests on evidence drawn from three distinct lines of research: (1) the direct evidence of fossil botany as to the geological succession of forms; (2) comparison of the stem anatomy in the two classes; (3) the study of the developing embryo within the embryo sac.

1. Direct historical evidence from the succession of fossil forms would of course be more conclusive than any based on comparative morphology. But unfortunately the geological record is particularly imperfect at the epoch which separates the gymnospermous flora of the Mesozoic age from the earliest fossil floras in which angiosperms can be recognized with certainty.³

2. The absence of a normal thickening ring in the stem of monocotyledons was formerly considered a primitive character. This was a very natural inference at a time when a normal cambium was unknown except among gymnosperms and dicotyledons. It led to the now discarded classification which united gymnosperms with dicotyledons, of which traces may still be found in systematic text-books.

But now that the anatomy of many fossil cryptogams is as well known as that of any living forms, we realize that cambial thickening was a commonplace in vegetable anatomy long before the advent of angiosperms. Some of the ancestors common to monocotyledons and dicotyledons must almost certainly have possessed it, and if so, its absence from the stem of monocotyledons must be regarded as the loss of a primitive character.

3. The argument from the history of the embryo within the embryo sac is that which has perhaps had the most weight with botanists. The facts are shortly these:

In both classes the cotyledons are commonly the first mem-

³SEWARD, A. C., Presidential address to Section K of the British Association. 1903.

bers differentiated from the mass of meristem which constitutes the embryo. Among monocotyledons the single cotyledon forms a club-shaped termination to the axis, and the boundary between these members is first clearly defined by the appearance of a lateral cleft within which is formed the growing-point of the stem. Thus the cotyledon is apparently terminal in monocotyledons, the stem bud lateral (*fig. 3* on p. 340).

In the dicotyledonous embryo a similar enlargement appears at one end, but it is sooner or later divided into two lobes by a median cleft, within which the stem bud is formed. As soon as this takes place the cotyledons appear lateral, the stem bud terminal.

The accepted interpretation of these facts is that the club-shaped enlargement of the dicotyledonous embryo before lobing begins is equivalent to that which gives rise to the single seed leaf of monocotyledons. Its subsequent bifurcation indicates the origin of both cotyledons from that of an ancestor which possessed but one. This interpretation has been recently urged by Mr. Lyon in his paper on *Nelumbium*.⁴ In this species the meristematic mass at the end of the embryo attains some size before it gives rise to a pair of cotyledons. The stem bud first appears in a lateral position with regard to it, and later reaches a symmetrical station between the cotyledons by degrees. The embryo is said by Mr. Lyon to pass through a monocotyledonous stage, and he is even prepared on the strength of these observations to class *Nelumbium* among monocotyledons. Professor Strasburger⁵ has observed with great force that the position of the embryo at one side of the embryo sac of *Nelumbium* has probably more to do with its one-sided development than any ancestral reminiscence.

A similar criticism may, I think, be applied to the whole argument. A parasitic mass of meristem which is forced to develop within very narrow limits naturally assumes the most convenient form, and any detail of shape is at least as likely to be due to its environment as to inheritance from remote ancestors.

⁴ LYON, H. L., Embryogeny of *Nelumbo*. Minnesota Bot. Studies 2 : 643. 1901.

⁵ STRASBURGER, E., Ein Beitrag zur Kenntniss von *Ceratophyllum submersum*. Jahrb. Wiss. Bot. 37 : 477. 1902.

This view is strengthened by what we know of the development of the embryo among pseudo-monocotyledons. Scattered here and there among normal dicotyledons are species, or small groups of species, which on germination show a single seed leaf. There is no doubt whatever as to the affinities of these forms. We can safely assume that at some geologically recent period the common ancestor from which sprang all the species in the genus *Corydalis*, for instance, must have possessed two distinct cotyledons. Most species of *Corydalis* still possess two, but *C. cava* and a few allied forms have but one. There can be no doubt here that the species with a single seed leaf are derived from an ancestor with two. It would seem that the early history of the embryo ought to throw light on the way in which this took place. In such a form as *Corydalis cava* we should expect to see the bifurcation begin in the very young embryo, and that the two members thus indicated would later be reduced to one, either by the abortion of one of them or by the union of both.

Hegelmaier⁶ described the formation of the embryo in several pseudo-monocotyledons in 1878. He worked out every detail in three species, beginning with the fertilized ovum and ending with the ripe seed. In each case he examined for comparison the embryos of closely allied species in which both cotyledons were present. His work has been completed by that of Sterckx⁷ and Schmid,⁸ who have traced the development of the embryo in those three species through its long period of maturation within the ripe seed down to the epoch of its germination.

In *Ranunculus Ficaria*, *Corydalis cava*, and *Carum Bulbocastanum* the history of the embryo from fertilization to germination is now complete. In all three species the cotyledon is single from the first. No bifurcation appears at any stage, though the cotyledon of *Ranunculus Ficaria* soon becomes—and remains—slightly two-lobed. The plumule is formed in a deep cleft which marks

⁶ HEGELMAIER, F., Vergleich. Unters. über Entwick. dicot. Keime. Stuttgart, 1878.

⁷ STERCKX, R., Recherches anat. sur l'embryon et les plantules . . . des Renonculacées. Mém. Soc. Roy. Sci. Liège III. 2:—. 1899.

⁸ SCHMID, Beitr. zur Embryo-Entwick. einiger Dicotylen. Bot. Zeit. 60: 207. 1902.

the level dividing the axis of the embryo from its cotyledon. But as the cotyledon develops it does not appear terminal as it commonly does among true monocotyledons. The plumule soon comes to lie in a straight line with the axis, and the cotyledon is a hollowed structure which partly surrounds it. Indeed, the whole embryo at this age closely resembles that of *Tamus* as described by Solms-Laubach, in which the cotyledon appears lateral from the first (*figs. 4, 5, 6*, p. 340).

Hegelmaier indeed describes a single abnormal embryo of *Carum Bulbocastanum* in which the lower lip of the usually lateral cleft containing the plumule attains some size, and he interprets this structure as the rudiment of a second cotyledon. Little weight can be attached to an isolated case of this kind. We do not even know whether the lump of tissue he figures would have become a leaf-like member. This is the only ground for considering the absence of a second cotyledon in any pseudo-monocotyledon as due to its early abortion. We may therefore fairly say that the comparative study of the young embryo in the genera *Ranunculus*, *Corydalis*, and *Carum* does not indicate the process by which a species within those genera has come to possess a single cotyledon where its ancestor had two.

The history of the embryo within the ovule and seed then throws no light on the comparatively simple problem of the derivation of such forms as *Corydalis cava*, *Ranunculus Ficaria*, or *Carum Bulbocastanum* from the ancestral *Corydalis*, *Ranunculus*, or *Carum*. This consideration casts great doubt on the value of similar evidence when we attempt the harder task of tracing the origin of monocotyledons from an ancestor far more remote.

To sum up, research conducted on the three lines hitherto considered does not afford evidence of any great value in favor of the superior antiquity of monocotyledons. On the other hand, it does not so far support the opposing claims of dicotyledons.

EVIDENCE FOR THE PRIMITIVE DICOTYLEDON.

Two observers, M. Quéva and Professor E. C. Jeffrey, have recently appealed to anatomical evidence of a kind hitherto neglected. M. Quéva has made a careful anatomical study of

several monocotyledons, including the liliaceous climber *Gloriosa superba*.⁹ In this species he finds a well-marked cambium within the bundles of the second-year tuber and of all succeeding tubers. Secondary elements are added to the xylem and phloem of each bundle by its cambium, which is active throughout the two seasons during which the tuber lasts. Moreover, the bundles in the climbing stem of the seedling possess a cambium, though the elements which it contributes to the xylem and phloem soon lose their radial arrangement by further growth. M. Quéva comes to the following conclusion: "La persistance de la zone cambiale dans certains faisceaux des Monocotylédonées prouve qu'il est logique de considérer ces plantes comme dérivant de Dicotylédonées inférieures par extinction précoce de la zone cambiale et par augmentation du nombre des faisceaux de la trace foliaire" (*l. c.*, p. 147).

It will be remembered that Miss Anderssohn in 1888 described a cambium in the bundles of the young stem of several monocotyledonous seedlings.¹⁰

Professor Jeffrey has recently expressed his phylogenetic conclusions without reserve: "In the present state of our knowledge we are apparently justified in considering the monocotyledons to be a modern, strictly monophyletic, and specialized group, derived from dicotyledons or their parent stock, possibly by adaptation in the first instance to an amphibious mode of life."¹¹

The evidence on which this view is based is the comparison of the mature stem anatomy with that of the seedling in what may be called the third period of its life. The first includes all the time during which the embryo is completely inclosed by the ovule or seed. The second period begins with germination, and while it lasts the seedling consists mainly of cotyledon, hypocotyl, and primary root. The young stem bud is present, but is

⁹QUÉVA, C., Contributions à l'anatomie des monocotylédonées. Mem. de l'Université de Lille. 1900.

¹⁰ANDERSSOHN, S., Ueber d. Entwickel. d. primären Gefässbündelstränge d. Monokotylen. Bihang till K. Sv. Vet. Akad. Handl. 12: 188 (Bot. Centralbl. 38: —. 1889).

¹¹COULTER and CHAMBERLAIN, Morphology of Angiosperms 316. 1903.

small compared with the cotyledon, and is usually more or less protected by it.

In the third period the stem bud becomes the ascending axis, and the cotyledon—even if persistent—is dwarfed by its rapid development. In the early part of its third period the plant is still very far from maturity. The epicotyl of monocotyledons contains at this time a single ring of collateral bundles, which may even show traces of a cambium. The stem, in fact, resembles that of a dicotyledon. In some monocotyledons the mature rhizome and the nodal regions of the aerial stem are characterized by amphivasal bundles. These are not found in the seedling (Jeffrey, *l. c.*).

There is nothing forced about the explanation of these facts given by Professor Jeffrey. As the characters of the young stem recall those of a dicotyledon, the features of monocotyledons appearing later in life, it is to be concluded that the stem anatomy of the common ancestor was essentially dicotyledonous. As has been said already, the anatomy of fossil cryptogams establishes a presumption that the primitive angiosperm possessed secondary thickening. The traces of the process found in the immature stem of monocotyledons strongly confirms this presumption.

For some years I have been employed on a comparative examination of monocotyledons soon after germination—as a rule during what I have called their second period of growth. About this epoch the vascular system of the immature structure is first completely defined by the lignification of the xylem.

This work has led me to the conclusion that monocotyledons are descended from an ancestor with two cotyledons, and that the single cotyledon which distinguishes them is a member formed by the fusion of the pair. For the nature and strength of the evidence I must refer to a previous paper.¹² It is sufficient to say here that the absence of a true midrib is a very general character in the cotyledon of monocotyledons, that its place is commonly supplied by two equivalent bundles, and that in the

¹²SARGANT, E., A theory of the origin of monocotyledons. *Annals of Botany* 17: 1. 1903.

more primitive forms these bundles are massive and very widely separated.¹³ The suggestion that each represented the midrib of an ancestral cotyledon seemed an adequate and simple explanation of the phenomenon, and it was much strengthened when I examined a number of dicotyledons—all from the Ranales—in which the cotyledons are partially united. The simplification of structure caused by this incomplete union was found to reduce the vascular symmetry of the ranal seedling (*Eranthis*, *Podophyllum*) to a skeleton much resembling that previously described as primitive among monocotyledons (*Anemarrhena*, *Albuca*).

An angiospermous plant possessing two seed leaves and exogenous stem structure would certainly, if now discovered, be ranked among dicotyledons, even though in other characters it should resemble a monocotyledon, or differ from both classes. Assuming an ancestor with these two characters, monocotyledons must be considered as derived from a dicotyledonous stock, not necessarily at one epoch or from a single strain. Can indications be found in the structure of living plants to suggest the conditions which operating for a length of time on such a stock might lead to the formation of a race or races essentially of the monocotyledonous type?

Beginning with the most general character and that which gives its name to the class, we may ask: Under what circumstances is the possession of a single cotyledon in place of two an advantage to the plant? An answer to that question is naturally sought among the few dicotyledons which possess but one seed leaf. I have compiled a list of species with this character.¹⁴

¹³The forms to which I refer are liliaceous: *Anemarrhena*, *Albuca*, and others nearly allied to these very distinct genera both in mature and in seedling characters. I believe them to be primitive among the Liliaceae after making a careful comparative study of seedlings from forty-five genera of that family. Systematists differ as to the position of the Liliaceae among monocotyledons. Some believe the type to be an ancient one from which many simpler monocotyledons are derived by reduction. My observations on the structure of seedling monocotyledons from a number of families incline me to accept this view, and on general grounds I prefer to attribute simplicity of structure when found in such advanced types as the angiosperm to reduction rather than antiquity. *Anemarrhena* and *Albuca*, then, if primitive among the Liliaceae are primitive also among monocotyledons in general.

¹⁴SARGANT, E., *l. c.*, p. 76.

They belong to eight genera which are systematically scattered, for they represent six families, Ranunculaceae, Fumariaceae, Umbelliferae, Primulaceae, Lentibularieae, Nyctagineae. Clearly these species cannot have inherited the peculiar form of their seedling from a common ancestor. It must be due to similar external conditions affecting certain species of very different descent in the same way.

One feature is common to all the pseudo-monocotyledons in my list—they all possess some underground member which is thickened into a tuber. In *Ranunculus Ficaria* one of the earlier cauline roots becomes tuberous; in the other species the hypocotyl is more or less thickened.

Moreover, the most complete list I can make of dicotyledons with their cotyledons partially united for some distance from the base upwards includes twenty genera.¹⁵ It contains but one genus—*Rhizophora*—in which the hypocotyl is not very much shortened, if not actually thickened. In the great majority the hypocotyl becomes a conspicuous tuber. The seeds of the single exception germinate under peculiar conditions,¹⁶ which would account for almost any amount of modification in the structure of the seedling.

The association of a tuberous habit with the reduction of the cotyledonary members has been noticed by several observers. Darwin in the *Movements of Plants*¹⁷ says: "From the several cases now given, which refer to widely distinct plants, we may infer that there is some close connection between the reduced size of one or both cotyledons and the formation, by the enlargement of the hypocotyl or of the radicle, of a so-called bulb."

Now the formation of a shortened and generally thickened rootstock, whether morphologically a stem or a root, is characteristic of the plants which Professor Areschoug¹⁸ has called geophilous. Such plants are found in regions where the conditions during part of the year are unfavorable to vegetation.

¹⁵SARGANT, E., *l. c.*, p. 73.

¹⁶KERNER and OLIVER, Natural History of plants 1: 602-4.

¹⁷DARWIN, C., The power of movement in plants 97. 1880,

¹⁸ARESCHOUG, Beiträge zur Biologie der geophilen Pflanzen. Lund, 1896.

During the winter of temperate, alpine, or arctic climates, during the prolonged drought of regions with a periodical dry season, such plants lose all their aerial organs and are left with the underground stock only. This is commonly a squat axis with roots and foliage buds—perhaps flower buds also—attached to it. A store of nourishment is always laid up in some part of this subterranean structure, as a rule in the enlarged stem.

The more rigorous the conditions, the more pronounced the adaptations to them. When the growing season is short, the flower of a geophyte often comes up with or before the leaves. No part of the genial weather is then lost with regard to the formation and ripening of the seed. When once ripe, the seed fears neither frost nor drought, but the seedling is less hardy. The great problem before a seedling which germinates under such conditions is how in the course of the short growing season it may best prepare to face the rigor of the coming months. Its first care is to form an underground storehouse in the shape of a swollen stem or root to which the food packed in the seed may be transferred. This store of food is plunged in the soil, at first by the downward growth of the seedling as it leaves the seed coats, and later by the contraction of the root system which drags the tuber lower still.¹⁹

In some species this is all that the seedling accomplishes in its first season (*Arum*, *Erythronium*,²⁰ *Veratrum*): it has lived on part of its food capital in order to place the rest in safety. But as a rule one, or even two, green leaves are sent up soon after germination, and then the contents of the storehouse are replenished by the activity of the assimilating surface.

The formation of assimilating organs in the seedling of a geophilous plant is, however, very greatly limited by the shortness of the growing season and the necessary formation of subterranean organs. Here lies the explanation we were seeking; the reduction of the cotyledons and the formation of a tuber are both adaptations to the geophilous habit.

Suppose a race of primitive angiosperms to be specialized as

¹⁹ RIMBACH, Ber. Deutsch. Bot. Gesell. 15:—. 1897.

²⁰ IRMISCH, Beitr. z. vergleichenden Morphologie der Pflanzen. Halle. 1854.

geophytes. Their originally distinct cotyledons become more and more closely united in order to economize material. In the end a single cotyledonary member is formed by their complete fusion. A monocotylous race might easily be derived in this way from one with two cotyledons.

But monocotyledons are distinguished from dicotyledons by other characters besides the single seed leaf. Taking these characters one by one, are they consistent with the hypothesis that monocotyledons were derived from a stock of dicotylous angiosperms by adaptation to the geophilous habit?

As has been said (p. 332), there are independent grounds for believing that monocotyledonous stem anatomy is derived from that of an ancestor framed on the dicotyledonous type. Modification of the ancestral stem structure in this direction might well follow on the gradual assumption by succeeding generations of the geophilous habit. For in every plant which passes part of the year underground a large foliage bud is formed on the subterranean stock in the course of a growing season, and this bud after remaining quiescent through the bad weather will push up as the next period of growth approaches. Such buds are formed even in the least specialized geophytes.

Scale leaves form the outer covering of such a bud; then follow the radical leaves which sometimes, but not always, surround the rudiment of an erect stem which will bear flowers as well as leaves. Scale leaves and radical leaves alike are broad-based; the insertion of each on the squat axis occupies a considerable segment of its circumference. When growth begins with the first genial weather, the axis does not elongate, or those basal internodes, at any rate, are suppressed which separate the whorls of scale leaves and of radical leaves from each other. The traces which enter the axis from those leaves fall naturally into concentric circles within it. In fact, they are at once arranged like the leaf traces of a monocotyledonous stem.

In many geophytes the parenchyma of the axis becomes a massive tissue packed with food stuff. This development of the tissue which surrounds them naturally tends to isolate the leaf traces from each other. The interfascicular cambium first dis-

appears, and then the cambial layer within each bundle, for no development of secondary elements is needed.

The structure of some living geophytes illustrates this process. In the first and second year tubers of *Eranthis*²¹ and *Arum*,²² for example, we find the slender leaf traces isolated among the abundant parenchymatous tissue which is packed with starch. The *Cyclamen* tuber is formed in a similar way.

Though this method of tuber formation is quite common, it is not universal. Jost's researches on *Corydalis solida*²³ show the tuber to be formed in this species by the activity of a normal cambium which adds a mass of parenchymatous elements to xylem and phloem alike. The reserve food is stored in the tissue thus produced. Each year sees a fresh tuber formed within that of last year, which it destroys. My own observations on first-year seedlings of *Anemone coronaria* and *Delphinium nudicaule* show that their tubers are formed in a similar way. The tissues—chiefly parenchymatous—which thicken them are added by a normal cambium. I have not examined older seedlings or mature plants.

Podophyllum offers the best example with which I am acquainted of a dicotyledon which, according to the present hypothesis, may be considered as arrested on the way to become a monocotyledon. A full account of the seedling and mature plant of *P. peltatum* is given in Mr. Holm's interesting memoir,²⁴ to which I must refer readers who wish for fuller detail. Owing to his kindness in sending me seeds, I have been able to examine the first-year seedling anatomically.

As in *Eranthus hiemalis*, the blades only of the cotyledons are distinct. Their petioles are united into a long tube, the base of which is beneath the surface of the soil. The hypocotyledonary axis is vertical and very short, but not swollen into a tuber. Its tissues are packed with starch. It is terminated

²¹SARGANT, E., *l. c.*, pp. 57-61, and *pl.* 6.

²²SCOTT and SARGANT. The development of *Arum maculatum* from the seed. *Annals of Botany* 12: 404-413. 1898.

²³JOST, Die Erneuerungsweise von *Corydalis solida* Sm. *Bot. Zeit.* 48:257. 1890.

²⁴HOLM, TH., *Podophyllum peltatum*. *BOT. GAZ.* 27:419. 1899.

above by the cotyledons and next year's bud; below by the primary root which is large, stout, and branched. At the end of the first year the stem bud is set free underground by the withering of the cotyledons, and in the following spring it throws up a single green member and adds a few very short internodes—separated by scale leaves—to the squat vertical axis underground. This axis is again terminated by a bud which will develop in the third season.

The plant continues to grow in this fashion for several seasons. Each year's period of activity adds a few very short internodes to the vertical subterranean axis and produces several scale leaves, together with one or two foliage leaves. At the end of four or five years a season comes in which the terminal bud remains dormant. The bud which develops is found at the end of a horizontal rhizome produced in the previous season from the axil of a scale leaf; it resembles the terminal bud in structure and in the leaves it bears. The flower-bearing stem arises from the axil of one of the upper leaves of such a bud.

The bundles of the flower-bearing stem and of the vertical axis are arranged in the scattered fashion characteristic of monocotyledons. The whole structure of the plant indicates that this is primarily due to the number of leaf traces entering an axis so greatly reduced in length. Within the lateral rhizome—which possesses elongated internodes and bears small scale leaves—the bundles are arranged in a single circle. The number of traces entering the axis from a single foliage leaf is indicated in *figs. 6 and 7* (Holm, *l. c.*, pp. 425–6). Cambial layers exist within each bundle, but the bundle sheaths are thick-walled, and there is no interfascicular cambium.

Thus in *Podophyllum* partially united cotyledons and a close approach to monocotyledonous stem anatomy are found in connection with the geophilous habit. The genus must be fairly ancient, as indicated by its rather isolated systematic position and the distribution of its species. Four are included in the *Index Kewensis*. One is found in the Himalayas, two in China, and the fourth in North America. Possibly it reproduces some of the characters found in an ancestor which had become some-

what differentiated from the primitive stock of angiosperms by adaptation to a geophilous habit, and was thereby tending to a monocotyledonous structure.

The development of the embryo within the embryo sac of monocotyledons has already been described at some length, and the value of the phylogenetic argument based on it has been criticised. Nevertheless, since great importance has been attached to the appa-

rently terminal position of the single cotyledon, it is worth while to consider how the facts appear from a new standpoint. If the cotyledonary member be derived from the two cotyledons of an ancestor, its rudiment cannot be really terminal, but must represent the congenital fusion of two lateral members. The terminal position is readily understood by compari-

son with such a seedling as that of *Delphinium nudicaule* (figs. 1 and 2).

In this species the leafy stem bud

develops in the same season as the cotyledons, and so soon as the first leaf attains any size it breaks through the cotyledonary tube near its base.

For a short time this leaf appears to be laterally inserted on the cotyledonary axis (fig. 1), but as the leafy

stem develops the cotyledons are pushed to one side, and then appear as a single lateral member (fig. 2). These errors are easily corrected; the stem bud is seen to be terminal, and the tube of the united cotyledons a fusion of two lateral members.

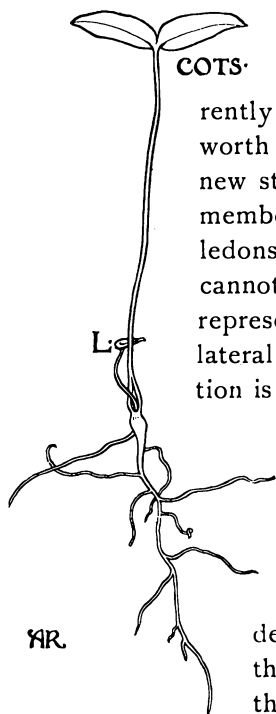


FIG. 1.—*Delphinium nudicaule*. Seedling eight weeks after seed was sown.

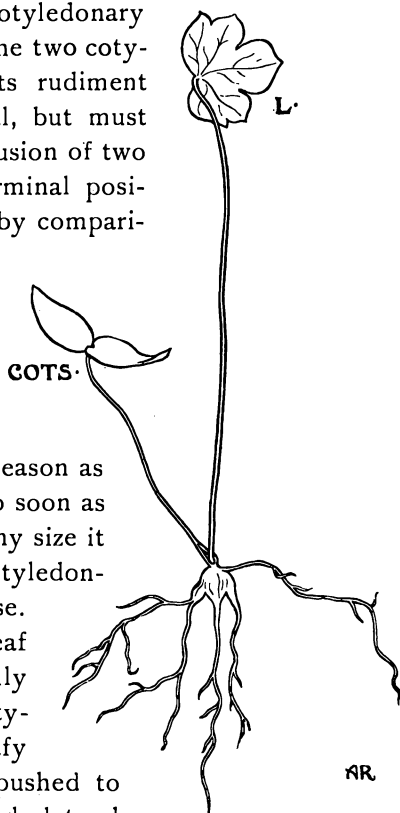


FIG. 2.—*Delphinium nudicaule*. Seedling fourteen weeks after seed was sown.

Now, suppose the cotyledons to become completely united by both margins, and that in the end this union is congenital. In order to develop freely, the stem bud must make its appearance at one side of the united members. As a rule, the cotyledons are differentiated some time before the growing point of the stem appears; in this case the single rudiment which represents both cotyledons is naturally formed in a straight line with the suspensor and the future axis. The rudimentary plumule when formed is forced to take up a lateral position (*Alisma*, *fig. 3*). As a rule, it attains the terminal position after germi-

ALISMA

CORYDALIS

TAMUS

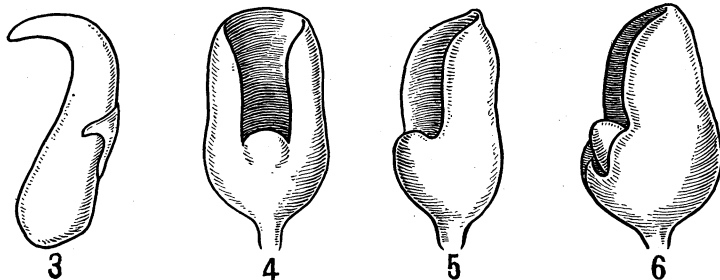


FIG. 3. *Alisma Plantago* (after HANSTEIN). FIGS. 4-5. *Corydalis cava* (after SCHMID); *fig. 4*, front view; *fig. 5*, side view. FIG. 6. *Tamus communis* (after SOLMS-LAUBACH):

nation, forcing the cotyledonary member to one side. In *Tamus* and *Commelina* the growing point of the stem appears terminal, the cotyledonary rudiment lateral, from the first²⁵ (*fig. 6*).

The single cotyledon in the ripe seed of *Corydalis cava* strikingly resembles that of *Tamus* in form and position (cf. *figs. 4* and *5* with *fig. 6*). The simplest explanation of both structures is that they represent the fusion of two ancestral cotyledons, but that on account of the early formation of the rudimentary plumule, or perhaps because the cotyledons have united by one margin only—as in *Ranunculus Ficaria*—the stem bud has never lost its terminal position.

This hypothesis accounts for the structure of the monocotyledonous embryo in a very simple way, and avoids the difficulty of

²⁵SOLMS-LAUBACH, Ueber monocotyle Embryonen mit scheitelbürtigem Vegetationspunkt. Bot. Zeit. 36:65. 1878.

supposing its single cotyledon to be a terminal leaf—a difficulty so formidable that the supporters of its terminal character have been obliged to assume that cotyledons are not true leaves, but organs *sui generis*. Their structure lends no support to this view.

The other characters which separate monocotyledons from dicotyledons are by no means so constant as the three already discussed; namely, the single cotyledon, the stem-anatomy, and the development of the embryo. Parallel venation of leaves, short duration of the primary root, and albuminous seeds are characters neither universal among monocotyledons nor confined to them. They are found in geophilous plants of both classes, though far more general among monocotyledons.

The value of these three subordinate characters as evidence in favor of the geophilous origin of monocotyledons is somewhat lessened by the consideration that they are found mainly—not exclusively—among geophilous genera within that class. They may be considered direct adaptations to the mode of life adopted by the species of their more recent ancestors, rather than an inheritance from geophilous ancestors common to all monocotyledons. The presence of all three characters among the palms, however—a family composed exclusively of trees—cannot be explained by recent adaptation to geophily. I shall return shortly to the evidence for the descent of all palms from a geophilous ancestor.

The trimerous symmetry of the flower is a very important character of monocotyledons, particularly to those botanists who derive the simpler flowers of the Aroideae, Gramineae, Palmae, and other orders from the more elaborate, considering their simplicity as due to the reduction of the floral parts. But I can discover no grounds for considering the trimerous flower as an adaptation to geophily. There may be an unsuspected connection, or the prevailing floral symmetry of monocotyledons may be an inheritance from the ancestral stock. A trimerous calyx and corolla is not uncommon among the Ranales.

To sum up, of the seven characters mentioned as distinguishing monocotyledons from dicotyledons, four have been shown to

occur frequently among geophytes and to be useful to the plant growing under conditions which determine the geophilous habit. They are therefore in all probability adaptations to that habit. Two more—the stem-anatomy and the apparently terminal cotyledon in the embryo—may be considered as direct consequences of such adaptations ; the stem anatomy acquiring its peculiar features from the insertions of numerous broad-based leaves on a squat subterranean axis, and the embryonic cotyledonary member arising from the congenital fusion of two ancestral cotyledons. The seventh character—trimerous floral symmetry—bears no obvious relation to the geophilous habit, but is not inconsistent with it.

In a paper read before the Linnaean Society in 1892, Mr. Henslow²⁶ maintains that monocotyledons were derived from dicotyledons by an adaptation to an aquatic habit. He bases his argument on the large proportion of monocotyledons which are aquatic, and on the nature of the characters, external and internal, which distinguish them from dicotyledons. These are on the whole, he suggests, the characters of water plants. He considers the single cotyledon as representing one of the dicotyledonous pair, the other having disappeared.

Other botanists have suggested the derivation of monocotyledons from an aquatic or amphibious ancestor. Some of their characters would bear this interpretation, and indeed aquatic plants have several features in common with geophytes. The main axis of the great majority of water plants is hidden in the mud of the river or lake bed, and the green parts in the colder climates die down on the approach of winter. The subterranean stem is commonly a rhizome, but it bears upright buds. When broad-based leaves are inserted on the shortened axis of such a bud, their traces might naturally be arranged in the scattered fashion actually found among the Nymphaeaceae (Henslow, *l. c.*, p. 512) and monocotyledons. But, on the other hand, the tendency of an aquatic habit is to reduce the vascular tissue altogether ; the leaf traces may almost disappear, and the vascu-

²⁶ HENSLow, G., A theoretical origin of endogens from exogens by self-adaptation to an aquatic habit. *Linn. Soc. Journ.* 29: 485. 1892.

lar system of the submerged stem be reduced to a slender central stele with hardly any lignified elements.

There are aquatic species with parallel-veined leaves (as *Valisneria*, *Zostera*), but this character is not common among water plants. It is almost confined to the monocotyledons among them. Circular or oval floating leaves, or the much dissected submerged leaves, are far more frequent.

The primary root of aquatic plants is often replaced early by tufted adventitious roots, a character found in many land plants with creeping rhizomes.

On the other hand, aquatic dicotyledons show no tendency to the formation of a single seed leaf in place of two, nor do they always possess albuminous seeds.

Great stress has been laid on the primitive floral structure displayed by many aquatic monocotyledons. Among the *Helioobiae* more than two whorls of stamens, and more than one whorl of carpels are not uncommon (*Stratiotes*, *Hydrocharis*, and others). Both stamens and carpels are occasionally indefinite in number and arranged spirally on the thalamus (*Alisma*, *Limncharis*, and others). It is very probable that such types reproduce the floral symmetry of ancestors which were intermediate in character between the *Ranales* and the *Liliiflorae*. But even if some primitive characters are retained by aquatic species, it does not follow that the primitive monocotyledon lived in the water, and that its descendants acquired their peculiarities by adaptation to that habit. It is more probable that the aquatic forms represent ancestors of our modern monocotyledons which were crowded out by the competition on land, and took refuge in the water, or on its edge, where competition was less severe.²⁷ The vegetative structure of such species would be modified by the change of environment and would no longer represent that of the ancestor, but the reproductive organs might well remain unchanged. Such ancestors, if geophilous, would readily adapt themselves to amphibious conditions; their underground stems creeping in the mud which fringed the pond or stream until by

²⁷ Cf. Darwin on the survival of ganoid fishes and simple vertebrates (*Origin of Species*, Sixth Ed. 1: 130, 154, 155, 163; 2: 99, 173. 1888.

degrees they grew beneath the water and sent up shoots more and more completely modified to an aquatic habit.

It has been objected that plants highly specialized to a particular mode of life, such as geophytes, are unlikely to give rise to a race so numerous and of such diversified form as monocotyledons. But the geophilous habit of a plant may be marked without any such profound modification in its structure as would destroy its capacity for adaptation to changed conditions. A geophyte is—as already suggested—particularly well suited to become amphibious. It acquires the climbing or twining habit with hardly less ease. *Bryonia dioica* and *Tamus communis*, two of our commonest perennial climbers, have very large tuberous rootstocks. Among the 187 genera mentioned in Bentham and Hooker's *Genera Plantarum* as belonging to the order Liliaceae, sixteen are mentioned as including species with a climbing or twining stem. Of these I find that eleven possess underground stems; rhizomes, tubers, or even bulbous, in the mature condition. Species from two of the remaining five I have examined as seedlings, and the rudiments of a tuber are very clear. Concerning the underground organs of *Rhipopozon*, *Semele*, and *Behnia* I have no information.

The absence of a normal cambium, which follows from the assumption of the geophilous habit, is certainly unfavorable to the production of trees. The want is occasionally supplied by the formation of anomalous thickening-rings (*Aloe*, *Dracaena*, etc.), but among the palms no such expedient is found. Without it they manage to grow into trees of great size in tropical and semitropical countries. Is it possible to trace the palms back to a geophilous ancestor?

Seedling palms are easily obtained, as they are much grown as pot-plants for indoor decoration. At this immature period of life they have many geophilous features. In the young seedling the hypocotyl is always short and commonly somewhat enlarged. The cotyledon sheathes the plumule more or less completely with its broad base. The first leaf of the stem bud is never more than a sheath; it is sometimes followed by one or two like itself before the first foliage leaf appears.²⁸ The stem at this time and

²⁸ MICHEELS, H., *Recherches sur les jeunes Palmiers, etc.* 105. Liège. 1889.

for many years later is a squat axis surrounded by successive leaf bases. The primary root is vigorous and persists for some time, but in the end it is always replaced by a number of much stouter cauline roots. In fact, if a young palm, such as is commonly sold for table decoration, be halved longitudinally, it is seen to be formed on the model of a bulbous plant. Its structure in youth may certainly be interpreted as a reminiscence of geophilous ancestry.

CONCLUSION.

In this account of a new view on the evolution of monocotyledons, I have tried to show that it is the most consistent—as in practice I have found it the most suggestive—among existing hypotheses.

An immense amount of work remains to be done on the structure, both external and internal, of seedlings before this or any other suggestion can be generally accepted as representing, even in outline, the real sequence of events. We need observers to carry on the work so well begun by Irmisch; monographs like those of Mr. Holm on *Podophyllum* and *Erigenia*; the detailed work of anatomists like Professor Jeffrey and M. Quéva. Even if no direct evidence should be contributed from the geological record, there is little doubt that the key to the descent of monocotyledons will be found in their morphology.

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